

EFFERENT INNERVATION OF THE VESTIBULE

A. Gribenski

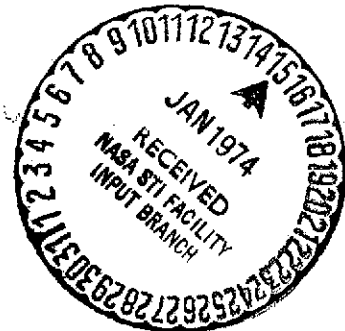
(NASA-TT-F-15232) : EFFERENT INNERVATION OF  
THE VESTIBULE (Scientific Translation  
Service) 21 p HC \$3 25 CSCL 06P

N74-13778

Unclas

G3/04 25364

Translation of: "L'innervation  
efférente du vestibule", Ann. Oto-  
Laryngol. Paris, Vol. 87, No. 1-2,  
1970, pp. 77-92.



## EFFERENT INNERVATION OF THE VESTIBULE

André Gribenski\*  
(Rouen)

### Organization of the efferent vestibular system

Neuroanatomy — The existence of efferent vestibular fibers, /77\*\* as indicated by Rossi and Cortesina (1965 a), has been accepted for the first time by Rasmussen (1946) and proved by Petroff (1955). He discovered a system of small diameter myelinated fibers in the internal ear of the cat, which lead to the vestibular receptors; these fibers degenerated upon sectioning the VIII<sup>th</sup> cranial nerve or upon a sagittal incision performed on the floor of the IV<sup>th</sup> ventricle which showed their central and moreover contralateral origin.

The centrifugal vestibular fibers were rediscovered by Rasmussen and Gacek (1958) and by Gacek (1960), also in the cat. Sectioning the vestibular root before its emergence (Figure 1) induces the degeneration of the disseminated fibers in the many branches of the vestibular nerve and proceeds to the sensory epithelium of the cristae and maculae (Figure 2). The same sectioning also reaches the olivo-cochlear fibers since they leave the bulb via the vestibular nerve (Gribenski, 1968); lesions existing in the lateral vestibular nuclei or Deiters nucleus (not the lesions concerned only with other nuclei) make the efferent vestibular fibers degenerate without affecting the cochlear fibers.

\*Professor in the Science Faculty of the University F-76, Rouen.

\*\*Numbers in the margin indicate pagination in the original foreign text.

Rasmussen and Gacek, opposing Petroff, did not obtain degeneration in the fibers stimulating the vestibule after sagittal sections on the floor of the IV<sup>th</sup> ventricle. From their observations, they concluded that the efferent vestibular fibers undoubtedly have their origin in the lateral vestibular nucleus of the same side.

After a labyrinthectomy in the cat, Carpenter, Baird and Alling (1959) found that retrograde degeneration occurred in cells situated in the median vestibular nucleus (dorsal vestibular nucleus, or Schwalbe nucleus), both superior (Bechterew nucleus) /78 and inferior — but not in the lateral nucleus — as well as cells situated in the fastigial nucleus of the cerebellum. They believe that vestibular nuclei and fastigial nuclei furnish the labyrinth with both direct and intersecting efferent fibers. The same results were obtained by a section of the VIII<sup>th</sup> nerve in the Macaque (Carpentier, 1960).

The existence of efferent vestibular fibers is thus established but there remain some uncertainties with respect to establishing their source in the vestibular nucleus and with respect to the proportion of direct and intersecting ones.

Robbins, Bauknight and Honrubia (1967) showed, by sectioning the VIII<sup>th</sup> nerve followed by wallerian degeneration, that the frog also had an efferent fiber system leading to various receptors in the vestibule. They thus confirmed, by a histological and anatomical method, the existence of the centrifugal vestibular innervation already shown in the frog by the electro-physiological method (Schmidt, 1963; Gleisner and Henriksson, 1964).

Electron microscopy — In the sensory epithelium of the cristae and maculae there are 2 categories of ciliated cells (type I and type II) differing by their shape and by the arrangement

of nerve endings in contact with them (Wersäll, 1956, 1960; Engström, 1958, 1960; Engström and Wersäll, 1958; Wersäll and /79 Flock, 1965). Both possess, like the ciliated cells of the organ of Corti, 2 types of nerve endings: very granular and non-granular (or slightly so). A calix, composed of a non-granular nerve ending, surrounds each type I ciliated cell. The granular endings are in contact with the calix. They are found in direct contact with the cellular membrane of the type II ciliated cells (Figure 3).

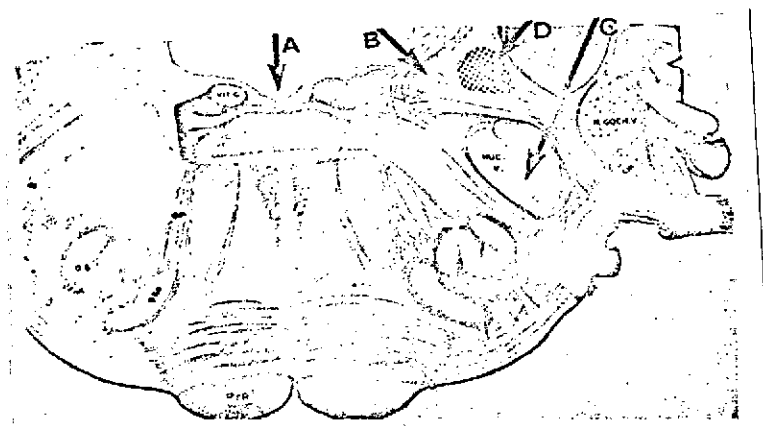


Figure 1. Transverse section of the rachidian bulb: A- placement of a section which determines the degeneration of intersecting olivo-cochlear fibers; B- placement of a section likely to produce degeneration in cochlear efferent fibers (the sections operated in A and B never induces degenerations among the nerve fibers of vestibular branches); C- section of a vestibular root, producing degenerations of vestibular and cochlear efferent fibers; D- placement of the lesions of lateral vestibular nuclei which induces degenerations in only vestibular efferent fibers; PYR- pyramidal fasciculus; OS, OSA- superior olivary nuclei; VII G- knee of the facial nerve; NUC. V- trifacial nuclei; N. COCH. V- ventral cochlear nuclei. According to R. Gacek, in Rasmussen and Windle, Neural mechanisms of the auditory and vestibular systems; Charles C. Thomas, publ., Springfield, Illinois (U.S.A.).

In the organ of Corti the granular endings belong to the efferent fibers and the non-granular endings, to the afferent fibers. We can believe the same arrangement occurs in the case of the

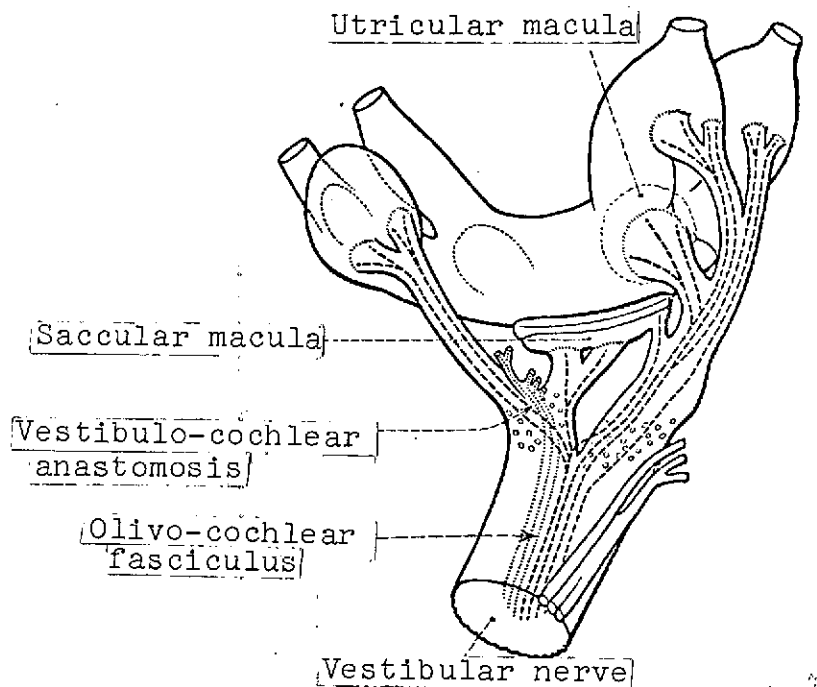


Figure 2. Distribution of the efferent fibers in various branches of the vestibular nerve.

... vestibular efferent fibers; - - - cochlear efferent fibers.  
According to R. Gacek, in Rasmussen and Windle, Neural mechanisms of the auditory and vestibular systems; Charles C. Thomas, publ., Springfield, Illinois (U.S.A.).

vestibular receptors (Wersäll, Gleisner and Lundquist, 1967), and this view is supported by the localization of specific acetylcholinesterase in the granular endings (Hilding and Wersäll, 1963).

Histochemistry — Histochemical studies have shown the /80 presence of acetylcholinesterase. The method of Koelle and Friedenwald (1949) or this technique slightly modified was used, notably by Holmstedt (1957): acetylcholinesterase activity gives rise to a brown-black precipitate of copper sulfide which permits precise localization of the enzyme on the cut. The presence of cholinesterase at the level of the nerve endings creates a strong suggestion of choline-energized transmission. On the other hand,

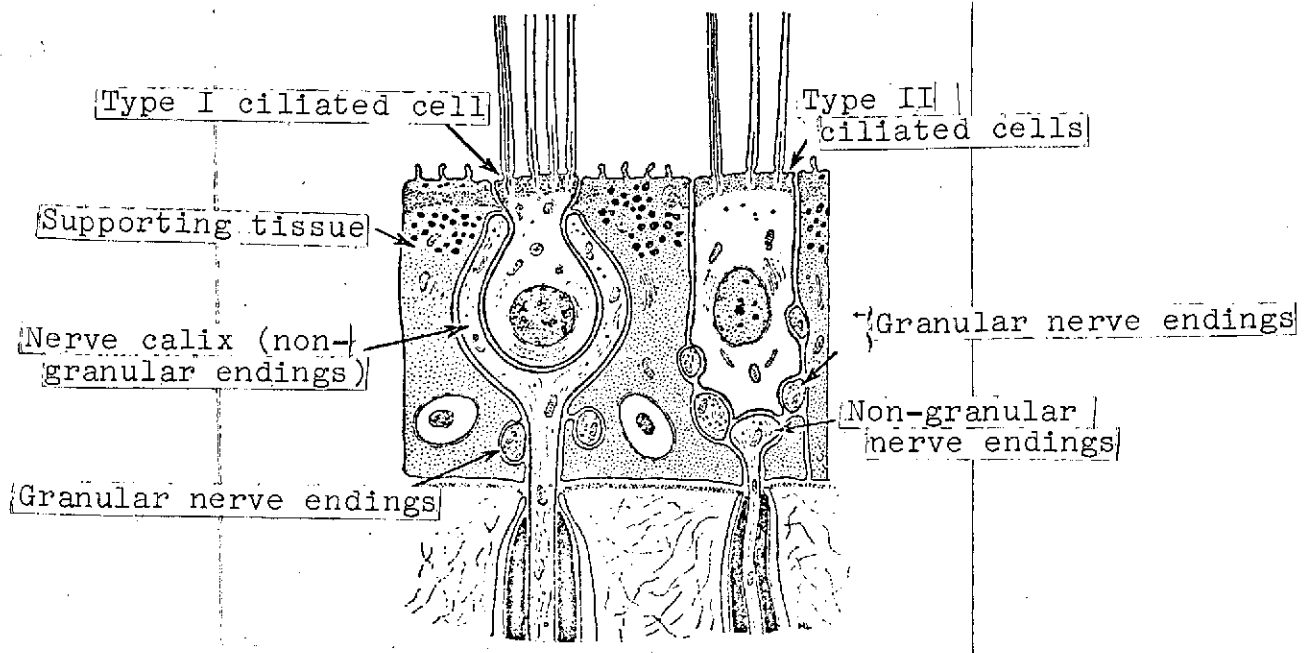


Figure 3. Schematic representation of 2 types of ciliated cells of vestibular sensory epithelia including their innervation.

According to H. Engström, in Rasmussen and Windle, Neural mechanisms of the auditory and vestibular systems; Charles C. Thomas, publ., Springfield, Illinois (U.S.A.).

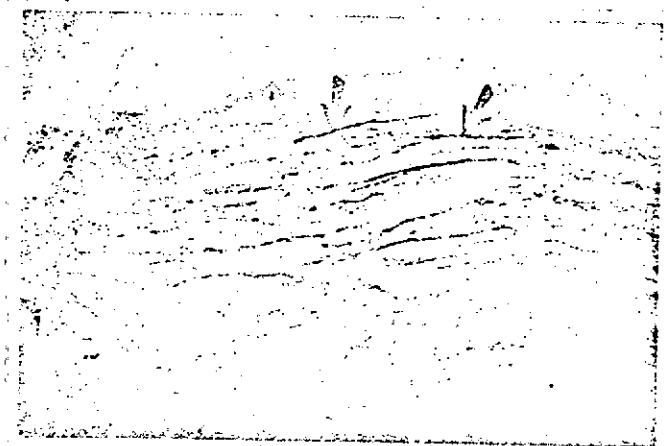


Figure 4. Ampullar nerve of the posterior semicircular canal. The arrows indicate 2 of the efferent fibers; these are colored brown-black by the method indicating activity in acetylcholinesterase agents. According to R. Gacek, Y. Nomura and K. Balogh, Acta Otolaryng. Vol. 59, 1965, pp. 541-553.

acetylcholinesterase does not exist or is found only in slight amounts in afferent nerve fibers; as a consequence, a large amount of acetylcholinesterase in a nerve fiber suggests considering it as efferent (Figure 4).

Dohlman, Farkashidy and Salonna (1958), then Dohlman (1960), were thus able to show the presence of acetylcholinesterase at the base of the sensory epithelium in the ampullar cristae and the utricular macula in the pigeon. In the cat, Ireland and Farkashidy (1961) found acetylcholinesterase at the same level /81 as those in the nerve endings surrounding the ciliated cells, but not in the cells themselves; moreover after section of the VIII<sup>th</sup> cranial nerve, it disappears in the time required to produce wallerian degeneration. Thus the efferent (or centrifugal) nature of the nerve fibers which contain and produce acetylcholinesterase is confirmed. According to the studies of Hilding and Wersäll (1962), these fibers correspond to the granular endings which are found, on the one hand, in contact with the nerve calices surrounding type I ciliated cells, and on the other hand, in contact with type II ciliated cells.

By the same method, Gacek, Nomura and Balogh (1965) were able to define the distribution of vestibular afferent fibers in the cat and confirmed the distribution already presented by Gacek (Figure 2). They indicate that there are 400 efferent fibers in the common stem of the vestibular nerve but they branch out before passing into the various branches of this nerve proceeding to the cristae and maculae.

The efferent fibers were again shown in the midst of the vestibular nerve in the guinea pig (Rossi, 1961), in the peripheral branches of this nerve in the guinea pig (Nomura, Gacek and Balogh, 1965), the squirrel monkey (Ishii, Murakami and Gacek, 1967) and man (Ishii, Murakami and Balogh, 1967). Through

research in acetylcholinesterase, the impregnation of silver in the bulbar neurons (Cajal's method) and the study of the retrograde cellular modifications after sectioning the VIII<sup>th</sup> nerve (Nissl coloration), Rossi and Cortesina (1962, 1963, 1965a and b) studied the fasciculi of the cochlear and vestibular efferent fibers in the guinea pig and rabbit; they did not find intersecting vestibular efferent fibers (Rossi, 1964).

#### Activity and function of the efferent vestibular system

/82

Effect of acetylcholine on vestibular receptors — The efferent fibers have been considered most likely choline-energetic. It is therefore important to learn the effects of acetylcholine on vestibular receptors. Rossi, Voena, [Buongiovanni and Cortesina (1964)] were able to introduce acetylcholine or an anticholinesterase agent into the endolymph by fistulization of the lateral canal in the rabbit. In many cases they obtained a horizontal-rotatory nystagmus whereby the rapid component was directed toward the opposite side of the ear. The nystagmus lasted a few minutes. It would seem plausible to deduce that an accumulation of acetylcholine at the ampullar cristae level of a semi-circular canal inhibits afferent nerve transmission. The same experiments revealed signs of an interdependence which maintained an equilibrium between the two vestibules. This interdependence could depend upon the activity of efferent nerve fibers.

Stimulation of the efferent vestibular system — The labyrinth of the frog is particularly favorable for experimentation due to the arrangement of the vestibular nerve where the various branches are easily accessible (Figure 5). Schmidt (1963), in removing the nerve of an ampulla or of an otolithic organ, collected efferent potentials on this nerve produced by bending a foot, by a pressure of the stomach or on the ocular orb, by stimulation of the semi-circular canals (Figure 6). Stimulation of an ampulla gave rise



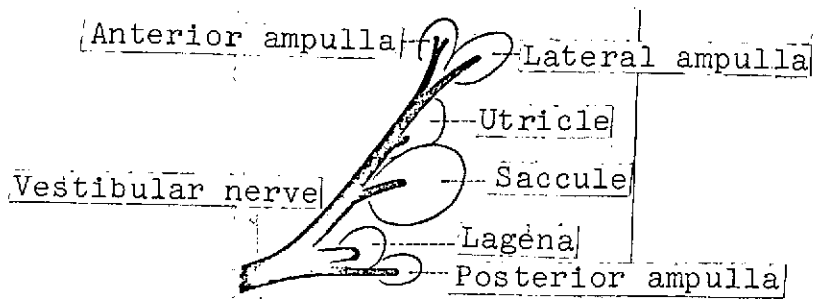


Figure 5. Innervation of the vestibular receptors in the frog.

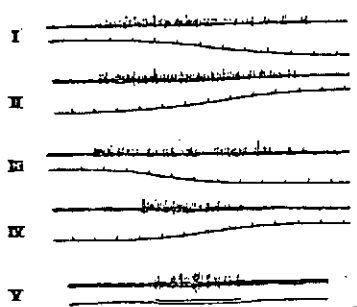


Figure 6. Efferent activity directed toward the anterior ampulla of the frog. The left anterior ampulla is detached from the ampulla and placed on an electrode; potentials of efferent activity run through them while the vestibular apparatus is stimulated by a movement. I- rotation about a vertical axis in the counter-clockwise direction; II- rotation in the clockwise direction; III- inclination movement toward the rear; IV- inclination movement toward the front or as certain other receptors are stimulated; V- (pressure on the animal abdomen). The line placed under the recording of the action potentials represents the stimulus. For I, II, III, and IV, it is first horizontal, then inclined (during the movement), finally horizontal again; this line carries the marks which constitute the time recordings (frequency: 10 per sec). In V, the double line indicates the duration of the stimulus.

The same stimulations produce similar action potentials directed toward the other ampullae and toward the otolithic receptors of the labyrinth. All the efferent action potentials disappear after sectioning the VIIIth nerve between the rachidian bulb and the otic capsule. According to R.S. Schmidt, *Acta Oto-laryng.* Vol. 56, 1963, pp. 51-64.

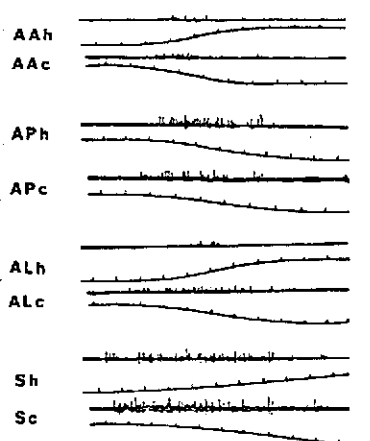


Figure 7. Efferent action potentials produced by the stimulation of the left lateral canal in the frog. The ampulla of the left lateral canal is stimulated by rotation; the efferent potentials are collected on various branches of the vestibular nerve, detached from the corresponding receptors. AAh- homolateral anterior ampulla; AAc- contralateral anterior ampulla; APh- homolateral posterior ampulla; APc- contralateral posterior ampulla; ALh- homolateral lateral ampulla (here, it is well understood, the nerve was only partially detached from the ampulla and we could only record one portion of its efferent activity. This recording then has the benefit of showing that the stimulation of a receptor can act on the receptor itself through the route of the efferent ampulla; Sh- homolateral saccule; SC- contralateral saccule.

The line appearing below each recording of the action potentials represents the rotation, by its inclined part. It carries marks which indicate the time (frequency: 10 per sec). According to R.S. Schmidt, *Acta Oto-laryng.* Vol. 56, 1963, pp. 51-64.

to efferent potentials being propagated towards all the homolateral and contralateral vestibular receptors, especially toward the stimulated ampulla itself (Figure 7). In a "Necturus" another genus of Batrachians, Schmidt (1965) similarly collected afferent vestibular potentials by stimulating the labyrinthine receptors with vibrations. Research by Gleisner and Henriksson (1964) confirm that the stimulation of a lateral ampulla by rotation in the frog, gives rise to efferent potentials on the lateral ampullar nerve of the opposite side.

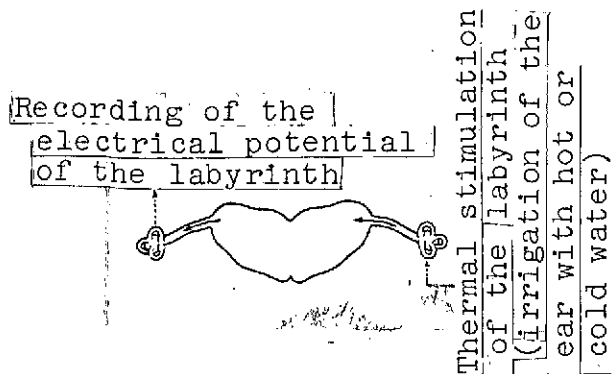


Figure 8. Stimulation of the right labyrinth modifies the rest potential of the left labyrinth. According to O. Sala, Acta Oto-laryng. Vol. 59, 1965, pp. 329-337.

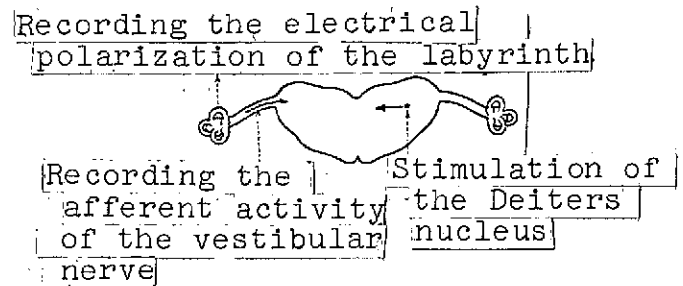


Figure 9. Faradic stimulation of Deiters nuclei of the right side produces a hyperpolarization of the left labyrinth and reduces the afferent activity of the left vestibular nerve. According to O. Sala, Acta Oto-laryng. Vol. 59, 1965, pp. 329-337.

It is also by electrophysiology that Sala (1964, 1965) showed the existence of efferent innervation of the vestibule in the cat. Thermal stimulation of a labyrinth (irrigation of the ear with warm or cold water) modifies the start of polarization (labyrinthic potential of rest) of the stimulated labyrinth and of the contralateral labyrinth (Figure 8). The faradic stimulation of Deiters nucleus on one side produces a hyperpolarization of the contralateral labyrinth. It also reduces the activity of the contralateral vestibular nerve (Figure 9), and therefore its spontaneous activity (Figure 10) and the activity due to a depolarization of the corresponding labyrinth by cathodic stimulation (Figure 11). These effects can only be due to a bringing into play of the efferent vestibular system because it disappears following a small displacement of the stimulating electrodes or of a sagittal section carried about on the floor of the IV<sup>th</sup> ventricle between the two Deiters nuclei. Afferent and efferent innervation of the vestibule forms circuits of retroaction. Efferent innervation also permits us to understand the interactions between the labyrinths, as well as the effects produced on the labyrinth and the contralateral vestibular nerve by the stimulation of a vestibular nucleus (Figure 12).

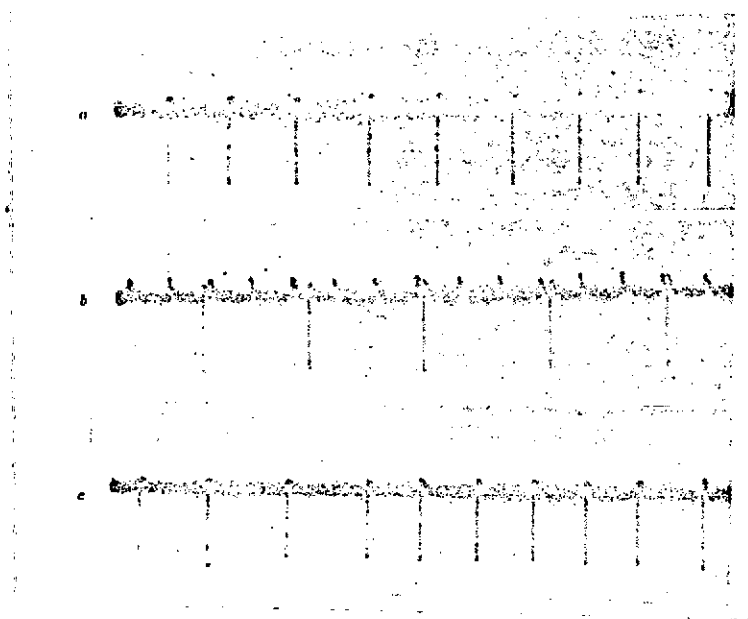


Figure 10. Reduction of spontaneous activity of the right vestibular nerve during the stimulation of the left Deiters nucleus.

a- spontaneous activity of an afferent unity of the right vestibular nerve; b- decrease in the activity during the stimulation of Deiters nucleus; c- spontaneous activity of the same fiber after the end of the stimulation of Deiters nucleus. According to O. Sala, Acta Oto-laryng., suppl. 197.

Bertrand and Veenhof (1964) collected efferent activity in the rabbit produced on the vestibular nerve by the stimulation of the contralateral labyrinth.

Role of the efferent vestibular system — Through clinical /86 observations and experimental research we know that the cerebral cortex, the sub-cortical centers, and the cerebellum influence the vestibular reflexes. Stimulation of the temporal cortex modifies the activity of vestibular nuclei. It increases the frequency of the discharge of certain neurons of the Deiters nucleus, while it inhibits other neurons of the same nucleus (Arslan and Molinari, 1965). The influence of the cortex and of the sub-cortical nuclei on the vestibulo-ocular reflex arc is

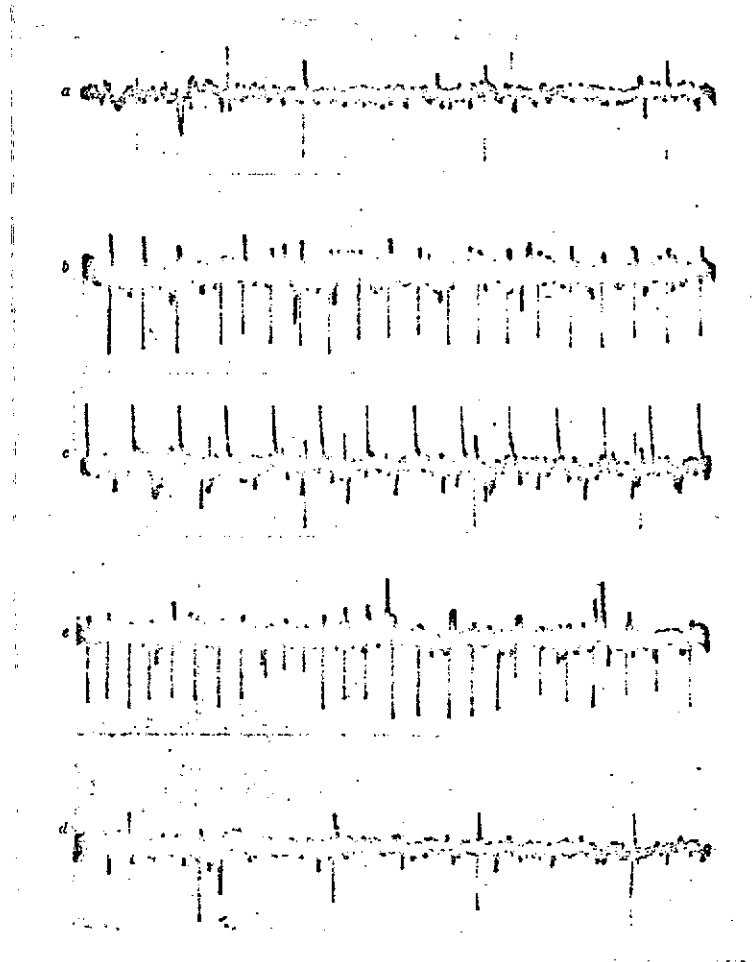


Figure 11. Reduction of activity of the right vestibular nerve during a stimulation of the left Deiters nucleus. a- spontaneous activity of the right vestibular nerve; b- activity of the same nerve responding to the depolarization of the corresponding labyrinth; c- reduction of this activity during the stimulation of Deiters nuclei (the regularly spaced spikes directed towards the top of this trace represents the stimulation); d- activity of the same vestibular nerve after the end of stimulation of Deiters nucleus (the depolarization of the labyrinth being maintained); e- spontaneous activity of the same nerve while we suppressed the depolarization of the labyrinth (the frequency of action potentials is sensibly the same as in a). According to O. Sala, *Acta Oto-laryng.*, suppl. 197.

partly produced at this level. It is possible that there also exists a control of the cortical and sub-cortical origin at the level of the oculo-motor nuclei. But we can equally ask whether the cortical, sub-cortical and cerebellar influence do not act

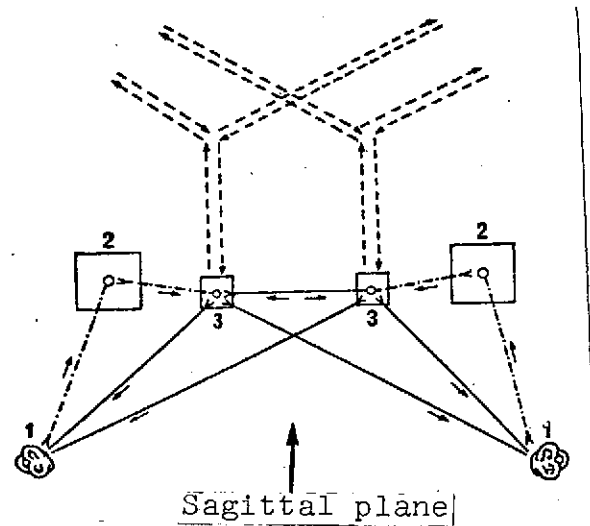


Figure 12. Diagram of the relationship between afferent and efferent vestibular innervations, according to Sala.

Solid lines- efferent vestibular fibers and connections between the 2 efferent vestibular systems; dashes and dots- efferent vestibular fibers; dashes- connections between the efferent vestibular system with the superior nerve centers; 1- vestibular receptors of two ears; 2 and 3- vestibular nuclei (2- first relay of the afferent vestibular routes; 3- source cells of the efferent vestibular system). According to O. Sala, Acta-laryng., suppl. 197.

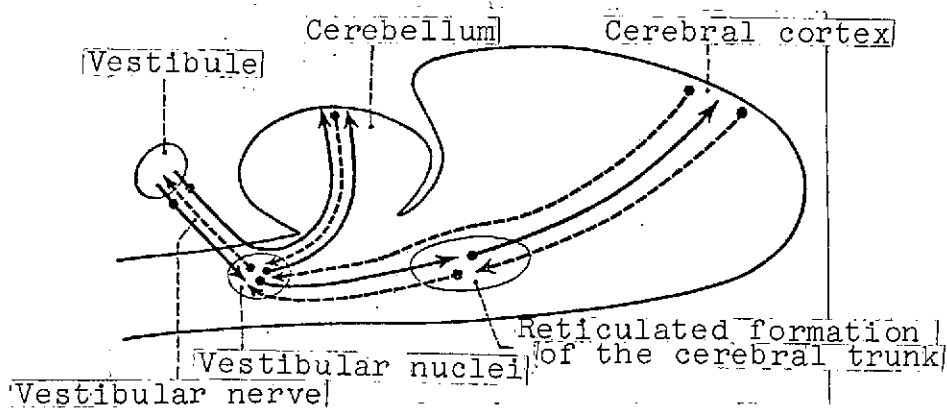


Figure 13. Nerve connections explaining the cortical, sub-cortical and cerebellar activities on the vestibular nuclei, and possibly on the vestibular receptors themselves.

Solid lines- afferent vestibular fibers, corticopetal and cerebellipetal fibers; dashes- corticifugal fibers, cerebellifugal fibers, efferent vestibular fibers. The vestibule forms part of the loops of retroaction which close at the level of the vestibular nuclei but also of other circuits closing at superior levels.

on the vestibular receptors themselves through the efferent fibers which arise from the vestibular nuclei (Gernandt, 1967). The connections which exist among the cerebral cortex, reticulated formations, cerebellum, vestibular nuclei and the vestibule, lead us to believe that there is a central regulation of the functioning of peripheral vestibular apparatus (Figure 13). It is also plausible that a retroaction loop exists with which the vestibule itself would participate in this regulation. We know that efferent mechanisms exist which are capable of inhibiting the activity of many receptors: olfactory bulb, retina, cochlea, neuro-muscular fasciculus. Undoubtably it is the same for the vestibule. This reminds us of the results of certain experiments by Sala (1964, 1965). In this case, the role of the efferent vestibular system — a role which has not been shown until presently (Giesen and Klinke, 1969) — could be to allow the control and the regulation of afferent messages coming from the semi-circular canals and otolithic organs. /87

On the other hand, Fluor (1961) states that a unilateral labyrinthectomy produces a facilitating effect on the preserved labyrinth, which is probably due to the suppression of an inhibitory influence exercised by one labyrinth on another (an influence which would necessarily utilize the route of efferent fibers). But this hypothesis remains to be examined in the light of experiments on animals. Following their observations on caloric and rotatory habituation, Fluor and Mendel (1962a and b, 1963, 1964a and b) believe that the efferent innervation could play a role in "habituation" (or adaptation) of the vestibular apparatus. This is also suggested by MacCabe and Gillingham (1964). Here again, we are dealing with a hypothesis. Adaptation is a central phenomenon and there could be other mechanisms to explain it.

## REFERENCES

1. Arslan, M. and G.A. Molinari. "Modifications of the Activity of the Vestibular Nuclei in the Cat, Following Stimulation of the Temporal Lobe." Acta oto-laryng., Vol. 59, 1965, pp. 338-343.
2. Bertrand, R.A. and V.B. Veenhof. "Efferent Vestibular Potentials by Canalicular and Otolithic Stimulations in the Rabbit." Acta oto-laryng., Vol. 58, 1964, pp. 515-524.
3. Carpenter, M.B. "Experimental Anatomical-Physiological Studies of the Vestibular Nerve and Cerebellar Connections," in: Rasmussen and Windle. "Neural Mechanisms of the Auditory and Vestibular Systems, Chap. 22." Charles C. Thomas, Publisher, Springfield, Illinois (U.S.A.), 1960.
4. Carpenter, M.B., D.S. Bard and F.A. Alling. "Anatomical Connections Between the Fastigial Nuclei, the Labyrinth and the Vestibular Nuclei in the Cat." J. Comp. Neur., Vol. 111, 1959, pp. 1-26.
5. Dohlman, G. "Histochemical Studies of Vestibular Mechanisms," in: Rasmussen and Windle. "Neural Mechanisms of the Auditory and Vestibular Systems, Chap. 19," Charles C. Thomas, publisher. Springfield, Illinois (U.S.A.), 1960.
6. Dohlman, G., J. Farkashidy and F. Salonna. "Centrifugal Nerve Fibers to the Sensory Epithelium of the Vestibular Labyrinth." J. Lar. Otol., Vol. 72, 1958, pp. 984-991.
7. Engström, H. "On the Double Innervation of the Sensory Epithelia of the Inner Ear." Acta Oto-laryng., Vol. 49, 1958, pp. 109-118.
8. Engström, H. "The Innervation of the Vestibular Sensory Cells." Acta Oto-laryng., Suppl. 163, 1960, pp. 30-41.
9. Engström, H. and J. Wersäll. "Structure and Innervation of the Inner Ear Sensory Epithelia." Intern. Rev. Cytol., Vol. 6, 1958, pp. 535-585.
10. Fluor, E. "Efferent Influence on Vestibular Function Following Unilateral Labyrinthectomy." Acta Oto-laryng., Vol. 53, 1961, pp. 571-577.



11. Fluor, E. and I. Mendel. "Habituation, Efference and Vestibular Interplay. I. Monoral Caloric Habituation." Acta Oto-laryng., Vol. 55, 1962a, pp. 65-80.
12. Fluor, E. and L. Mendel. "Habituation, Efference and Vestibular Interplay. II. Combined Caloric Habituation." Acta Oto-laryng., Vol. 55, 1962b, p. 136.
13. Fluor, E. and L. Mendel. "Habituation, Efference and Vestibular Interplay. Threshold After Habituation, Habituation of Horizontal and Vertical Semi-Circular Ducts." Acta Oto-laryng., Vol. 56, 1963, pp. 521-522.
14. Fluor, E. and L. Mendel. "Habituation, Efference and Vestibular Interplay. III. Unidirectional Rotatory Habituation." Acta Oto-laryng., Vol. 57, 1964a, pp. 81-88.
15. Fluor, E. and L. Mendel. "Habituation, Efference and Vestibular Interplay. IV. Rotatory Habituation of the Vertical Semi-Circular Canals." Acta Oto-laryng., Vol. 57, 1964b, pp. 459-464.
16. Gacek, R. "Efferent Component of the Vestibular Nerve," in: Rasmussen and Windle. "Neural Mechanisms of the Auditory and Vestibular Systems, Chap. 20;" Charles C. Thomas, publisher. Springfield, Illinois (U.S.A.), 1960.
17. Gacek, R., Y. Nomura and K. Baloch. "Acetylcholinesterase Activity in the Efferent Fibers of the Stato-Acoustic Nerve." Acta Oto-laryng., Vol. 59, 1965, pp. 541-553.
18. Gernandt, B.E. "Central Regulation of the Vestibular System." Arch. Oto-laryng., Vol. 85, 1967, pp. 521-528.
19. Giesen, M. and R. Klinke. "Directional Characteristics of Primary Afferences of the Otolith Organ for Intect Efference Innervation." Acta Oto-laryng., Vol. 67, 1969, pp. 49-56.
20. Gleisner, L. and N.G. Henriksson. "Efferent and Afferent Activity Pattern in the Vestibular Nerve of the Frog." Acta Oto-laryng., Suppl., 192, 1964, pp. 90-103.
21. Gribenski, A. "Efferent Innervation of the Cochlea and its Role." Ann. Oto-laryng. Paris, Vol. 85, 1968, pp. 511-523.
22. Hilding, D. and J. Wersäll. "Cholinesterase and its Relation to the Nerve Endings in the Inner Ear." Acta Oto-laryng., Vol. 55, 1962, pp. 205-217.

23. Holmstedt, B. "A Modification of the Thiocolin Method for Determination of Cholinesterase." *Acta physiol. scand.*, Vol. 40, 1957, pp. 332-337.
24. Ireland, P.E. and J. Farkashidy. "Studies on the Efferent Innervation of the Vestibular End Organs." *Ann. Otol.*, Vol. 70, 1961, pp. 490-503.
25. Ishii, T., Y. Murakami and K. Balogh. "Acetylcholinesterase Activity in the Efferent Nerve Fibers of the Human Inner Ear." *Ann. Otol.*, Vol. 76, 1967, pp. 69-82.
26. Ishii, T., Y. Murakami and R. Gacek. "Histochemical Study of the Acetylcholinesterase Activity in the Inner Ear of the Squirrel Monkey." *Acta Oto-laryng.*, Vol. 64, 1967, pp. 267-279.
27. Koelle, G.B. and J.S. Friedenwald. "A Histochemical Method for Localizing Cholinesterase Activity." *Proc. Soc. Exp. Biol.* New York, Vol. 70, 1949, pp. 617-622.
28. Mac Cabe, B.M. and K. Gillingham. "The Mechanism of Vestibular Suppression." *Ann. of Otol., Rhinol. and Laryng.*, Vol. 73, 1964, pp. 816-828.
29. Nokura, Y., R. Gacek and K. Balogh. "Efferent Innervation of Vestibular Labyrinth." *Arch. Otolaryng.*, Vol. 81, 1965, pp. 335-339.
30. Petroff, A.E. "An Experimental Investigation of the Origin of Efferent Fiber Projections to the Vestibular Neuro-Epithelium." *Anat. Rec.*, Vol. 121, 1955, pp. 352-353.
31. Rasmussen, G.L. "The Olivary Peduncle and Other Fiber Projections of the Superior Olivary Complex." *J. Comp. Neur.*, Vol. 84, 1946, pp. 141-220.
32. Rasmussen, G.L. and R. Gacek. "Concerning the Question of an Efferent Fiber Component of the Vestibular Nerve of the Cat." *Anat. Rec.*, Vol. 130, 1958, pp. 361-362.
33. Robbins, R.G., R.S. Bauknight and V. Honrubia. "Anatomical Distribution of Efferent Fibers in the VIII<sup>th</sup> Cranial Nerve of the Bullfrog (*Rana Catesbeiana*). *Acta Oto-laryng.*, Vol. 64, 1967, pp. 436-448.
34. Rossi, G. "Acetylcholinesterase During the Course of Development of the Internal Ear of the Guinea Pig." *Acta Oto-laryng.*, Suppl. 170, 1961.

35. Rossi, G. "Efferent Innervation of Vestibular Receptors." *Acta Oto-laryng.*, Vol. 58, 1964, pp. 230-238.
36. Rossi, G. and G. Cortesina. "The Efferent Innervation of the Inner Ear." *Panminerva med.*, Vol. 4, 1962, pp. 478-500.
37. Rossi, G. and G. Cortesina. "Research on the Efferent Innervation of the Inner Ear." *J. Laryng.*, Vol. 77, 1963, pp. 202-233.
38. Rossi, G. and G. Cortesina. "The Efferent Innervation of the Ear. A Historical-Bibliographical Survey." *Laryngoscope*. Vol. 75, 1965a, pp. 212-235.
39. Rossi, G. and G. Cortesina. "The Efferent Cochlear and Vestibular System in *lepus cuniculus* L." *Acta anat.*, Vol. 60, 1965b, pp. 362-381.
40. Rossi, G., G. Voena, S. Buongiovanni and G. Cortesina. "Experimental Studies on the Local Effects of Acetylcholine, Anticholinergic Substances and Cholinesterase Inhibitors on Vestibular Function." *Acta Oto-laryng.*, Vol. 58, 1964, pp. 159-174.
41. Sala, O. "The Efferent Vestibular System. Electrophysiological Research." *Acta Oto-laryng.*, Suppl. 197, 1964.
42. Sala, O. "Vestibular Efferent System." *Acta Oto-laryng.*, Vol. 59, 1965, pp. 329-337.
43. Schmidt, R.S. "Frog Labyrinthine Efferent Impulses." *Acta Oto-laryng.*, Vol. 56, 1963, pp. 51-64.
44. Schmidt, R.S. "Amphibian Acoustico-Lateralis Efferents." *J. Cell. and Comp. Physiol.*, Vol. 65, 1965, pp. 155-162.
45. Wersäll, J. "Studies on the Structure and Innervation of the Sensory Epithelium of the Cristae Ampullares in the Guinea Pig." *Acta Oto-laryng.*, Suppl. 126, 1956, pp. 1-85.
46. Wersäll, J. "Electron Micrographic Studies of Vestibular Hair Cell Innervation," in: Rasmussen and Windle. "Neural Mechanisms of the Auditory and Vestibular Systems, Chap. 18;" Charles C. Thomas, publisher, Springfield, Illinois (U.S.A.), 1960.
47. Wersäll, J. and A. Flock. "Functional Anatomy of the Vestibular and Lateral Line Organs," in: W.D. Neff. "Contributions to Sensory Physiology," Academic Press, New York, Vol. 1, 1965.

48. Wersäll, J., L. Gleisner and P.G. Lundquist. "Ultrastructure of the Vestibular and Organs," in: A.V.S. de Reuck and Knight. "Myotatic, Kinesthetic and Vestibular Mechanism, Ciba Foundation Symposium: J. and A. Churchill Ltd. London, 1967.

Translated for National Aeronautics and Space Administration under contract No. NASw 2483, by SCITRAN, P.O. Box 5456, Santa Barbara, California, 93108

|  |  |  |           |
|--|--|--|-----------|
| 1. Report No.<br>NASA TT F-15,232  | 2. Government Accession No.                          | 3. Recipient's Catalog No.                                 |           |
| 4. Title and Subtitle<br>EFFERENT INNERVATION OF THE VESTIBULE   |  | 5. Report Date<br>January, 1974                            |           |
|  |  | 6. Performing Organization Code                            |           |
| 7. Author(s)<br>André Gribenski  |  | 8. Performing Organization Report No.                      |           |
|  |  | 10. Work Unit No.  |           |
| 9. Performing Organization Name and Address<br>SCITRAN<br>Box 5456<br>Santa Barbara, CA 93108  |  | 11. Contract or Grant No.<br>NASw-2483                     |           |
|  |  | 13. Type of Report and Period Covered<br>Translation       |           |
| 12. Sponsoring Agency Name and Address<br>National Aeronautics and Space Administration<br>Washington, D.C. 20546  |  | 14. Sponsoring Agency Code                                 |           |
| 15. Supplementary Notes<br>Translation of: "L'innervation efférente du vestibule", Ann. Oto-laryng. Paris, Vol. 87, No. 1-2, 1970, pp. 77-92.  |  |  |           |
| 16. Abstract<br><br>From an extensive review of the recent literature, the authors attempt to clarify the following relationships: afferent and efferent vestibular innervations; nerve connections involving the cortical, sub-cortical and cerebellar activities and their influence on vestibular nuclei. |  |  |           |
| 17. Key Words (Selected by Author(s))  |  | 18. Distribution Statement<br><br>Unclassified - Unlimited |           |
| 19. Security Classif. (of this report)<br>Unclassified   | 20. Security Classif. (of this page)<br>Unclassified | 21. No. of Pages<br>20                                     | 22. Price |